The insect/plant relationship—an evolutionary perspective

T.R.E.SOUTHWOOD

Department of Zoology and Applied Entomology, Imperial College, London, S.W.7

In setting us the task of reviewing the insect/plant relationship at this meeting, the Society has challenged us to consider the evolution, nature and mechanism of a large proportion of the links in terrestrial ecosystems. I see my task as to try to establish a framework and to sketch out the length and breadth of this extensive subject. The outer limits, in taxonomic terms, pose the first problem: although most of us would agree to differ over the precise limits of the Insecta and whether this is synonymous with the class Hexapoda, the term plant, although conjuring up the idea of a seed plant (Spermatophyta), is strictly speaking applied to the whole Plant Kingdom.

Initially, I will endeavour to classify the various interactions and then turn to a review of the taxonomic distribution and major relationships as they have been successively forged and shaped under the pressure of natural selection.

Types of insect/plant relationship

The insect/plant relationship may basically be in terms of shelter, food or transport. The relative importance of these different links for insects and Spermatophyta is set out in Table 1; this shows that the most frequent inter-relationships are of three types: plants

Table 1. Insect/plant (Spermatophyta) relationships—the relative importance of different links

	Food	Shelter	Transport
Plants for insects	Major	Major	Very minor
Insects for plants	Minor	Minor	Major

providing food and/or shelter for insects, whilst the mobility of the latter has led to the evolution of plants' dependence on them for the transport of pollen and propagules. Most of the major orders of angiosperms are largely or entirely insect pollinated, with the exception of the Glumiflora (grasses and sedges), although even here entomophilous species occur (Leppik 1955). How plants attract insects to them is reviewed by Yeo*

* References in small capital letters refer to other papers in this volume

(1972); floral structures and insect pollinators exhibit remarkable co-evolution (Leppik 1957). The spread of the propagules of lower plants, especially fungi, bacteria and viruses, is a complex evolutionary interaction; in many cases, as with ambrosia beetles and fungi, the relationship is symbiotic (Baker 1963), or it may be of no significance to the insect (e.g. *Nematospora* transmitted by *Dysdercus* (Pearson 1958)). Certain workers have suggested that at least some plant viruses were originally insect pathogens (Jensen 1959; Maramorosch 1963), whilst Kennedy (1951) has formulated the hypothesis that they were originally insect secretions; their presence or absence can influence the range of host plants of a vector. The origin of this relationship is discussed by TINSLEY (1972). Insects are less frequently concerned with transportation of propagules of angiosperms although, for some plants, ants have an important rôle (Sernander 1906). An example of some of the very few cases where plants provide direct (as opposed to indirect, e.g. on floating herbage) transport for insects is the gorse weevil, *Apion ulicis* (Forst.), that is expelled from the ripe seed pods with the seeds (Davies 1928*a*).

Much of insect pathology is devoted to viruses, bacteria and fungi that feed on insects (Steinhaus 1946, 1963), but relatively few angiosperms are insectivorous: the genera *Pinguicula*, *Drosera*, *Utricularia* and *Nepenthes* are well known (Haberlandt 1914; Lloyd 1942; Juniper & Burras 1962; Schnepf 1966; Martin & Juniper 1970) and in some of the terrestrial genera the habit has probably evolved as an extension of the glandular hair type of 'defence mechanism'.

Large numbers of micro-organisms shelter within and upon insects, and algae are sometimes found on some aquatic species. Gressitt, Aoki & Samuelson (1966) described terrestrial weevils of the genus *Gymnopholus* from Papua that support epiphytic fungi, algae, lichens and liverworts on their elytra; these in turn harbour mites, rotifers, nematodes and bacteria.

When insects shelter on, or even more so when they are within, plants they are often protected from their enemies. Conversely, colonies of various ants, e.g. *Oecophylla* and *Pseudomyrmex*, protect the plants on which they rest by attacking phytophagous insects, browsing mammals and even nearby plants of other species (Way 1953*b*; Janzen 1966, 1967*a*; Hocking 1970); in the case of the acacia thorn ants, *Pseudomyrmex*, a complex symbiotic relationship has developed between the ant and its host tree and thus, although the plant provides physical shelter for the ant, the latter 'defends' the plant from browsers, competitors and even partly against fire. Janzen (1967*b*) showed that by removing potential competitors from around acacias, the ants may also produce a fire break.

SPERMATOPHYTA AS FOOD AND SHELTER FOR INSECTS

These are the major inter-relationships (Table 1) and clearly they have been evolving at least since the Permian when both groups suddenly appear in numbers in the fossil records. SMART & HUGHES (1972) review the evolutionary steps from the palaeontological angle. I want to analyse the nature and taxonomic distribution of these links, as observed today, from an evolutionary perspective. The phrase 'insect/plant relationships' conjures up a mental picture of locusts, caterpillars or aphids feeding and living on the outside of plants; this is generally thought of as a fairly frequent relationship. I want to show that *taxonomically speaking* it is most unusual, and that there are good evolutionary reasons why this should be so.

Taxonomic distribution and evolution of spermatophyta-feeding in terrestrial arthropods

The distribution of feeding habits in the various orders of insects and major groups of terrestrial arthropods is shown in Table 2. The first conclusion to be drawn is that the habit of feeding on dead and decaying material is the most widespread. Normally this material is contaminated by micro-organisms, and often the arthropod may have sym-

Table 2. Feeding habits of terrestrial arthropods (excluding blood sucking and pollen feeding)
*=major; +=minor

	Scavengers microbial feeders	Carnivorous	Fungi	Algae/lichens	Mosses/ferns	Spermatophyta
Onychophora		*				
Terrestrial Crustacea	*	+		+		
Arachnida Acari	*	*	+			*
other groups	+	*				
Chilopoda		*				
Diplopoda	*					
Symphyla	*				+	+
Pauropoda	*		+			
Protura	*					
Diplura	*	*				
Collembola	*	+	*	*		+
Thysanura	*					
Ephemeroptera	*	+				
Odonata		*				
Plecoptera	*	*		*		
Grylloblattodea	*					
Dictyoptera	*	*				
Orthoptera	*	*		*	+	*
Dermaptera	*	*				
Phasmida						*
Embioptera	*	*				
Zoraptera			*			
Isoptera	*					
Psocoptera	+		*	*		
Hemiptera		*	+	+	+	*
Thysanoptera	+	*	*			*
Mecoptera	*	*				
Neuroptera		*				
Trichoptera	*	*		+		+
Lepidoptera	+	+	+	+	+	*
Coleoptera	*	*	*	+	+	*
Hymenoptera	+	*	+		+	*
Diptera	*	*	*	+	+	*
Totals Major	21	19	6	4	0	9
Minor	5	4	5	6	8	3

biotic organisms in its gut (Brooks 1963; Buchner 1965). It seems that the sort of 'brew' that results from the activities of micro-organisms is well able to meet the nutritional requirements of the archaic terrestrial arthropod, and this feeding habit is of frequent occurrence in what are generally regarded as the less highly evolved groups, as well as in the higher orders. Even apparent plant feeders may fall into this category: Friend, Salkeld & Stevenson (1959) found that larvae of the onion fly (*Hylemyia antiqua* (Meig.)) were unable to live on sterilized onion tissue, but developed at a maximum rate when a *Bacillus* species was added to the diet. That micro-organisms *do* provide dietary requirements for insects is also shown by the many instances where simple synthetic diets are successful only after yeast or a yeast extract is added (e.g. Beck, Lilly & Stauffer 1949).

Turning to the two major 'secondary feeding habits', predation and feeding on Spermatophyta, it is seen that less than a third of the major evolutionary pathways (as represented by taxa of ordinal or higher level) have achieved the ability to feed on seed plants. When one considers that in most ecosystems the greatest proportion of the stored energy is available in the standing crop of seed plants (Table 3), it is noteworthy that only

TABLE 3. Annual production of biomass (in Kcal/m^2) of herbivores and plants (above ground) in different ecosystems (from Wiegert & Evans 1967)

	Fields Carolina	Old fields Michigan	Salt marsh Georgia	Grassland Tanganyika
Plants	1075	1360	6585	747
Herbivores	4·7	0·9	81	3·1

nine groups can utilize this source, whereas nineteen can utilize the relatively scarcer source of living invertebrates, which presents the additional difficulty of capture. Indeed we must conclude that adaptation to feeding and living on Spermatophyta presents certain difficult evolutionary 'hurdles'. Remembering that 'the host plant is not merely something fed on, it is something lived on' (Kennedy 1953), it seems that these 'hurdles' are: (a) nutritional, (b) attachment or 'holding-on', (c) desiccation, (d) host finding, including synchronization of life cycles.

The last three hurdles also face predators that live on large plants, whilst host- or food-finding requires special adaptations in almost all animals.

Nutritional 'hurdle'

Fraenkel (1953) took the view that all plants provide adequate nutrients for insects; in the light of increased knowledge of insect nutrition he has somewhat modified this viewpoint (Fraenkel 1969). Gordon (1961) and Schoonhoven (1969*b*) have expressed the view that host plants are often nutritionally sub-optimal. I would go further and suggest that the step from the original primitive scavenging/micro-organism feeding to plant feeding is nutritionally more difficult than that to predation and that this is the main basis for the comparative figures in Table 2. Three types of evidence can be considered:

(a) comparison of biochemical compositions and dietary requirements;
(b) the effects of changes in host-plant composition on insect development and fecundity;
(c) comparison of the conversion efficiencies of insects on different types of food.

Comparison of biochemical composition and dietary requirements Gross comparisons are difficult to interpret and can be dangerous. However, from our knowledge of insect nutrition and a comparison of various plant tissues with their other foods (Table 4), it

TABLE 4. Comparison of composition of various plant materials and insects (T = trace) (modified from Norman 1936; Spector 1956; Cross 1966; Lord 1968; Boyd 1970)

	% Fresh wt		% Dry wt	
	Water	Protein	Protein	Fat
Leaves				
Lettuce (*Lactuca*)	95	1·1	23	T
Watercress (*Nasturtium*)	91	2·9	32	T
Cabbage (*Brassica*)	90	2·7	27	T
Barley (*Hordeum*)			23	T
Rye (*Lolium*)			10	
Peanut (*Arachis*)			38	T
Reedmace (*Typha*)			4	
Waterweed (*Ceratophyllum*)			17	
Seeds				
Peas (*Pisum*)	79	5·8	28	T
Barley (*Hordeum*)			13	T
Pollen				
Willow (*Salix nigra*)	12·3	22	25	4·6
Pine (*Pinus*)	11·2	13	15	2·3
Micro-organisms				
Chlorella			62	?
Brewers' yeast	75	13	52	2
Bacillus			61	?
Insects				
Tenebrio larva	64	15	41	31
Sminthurus	70	18	58	90
Lepidopterous larva	80	9	45	18
Formicid	68	18	55	6·1

seems probable that two groups of substances have provided particular problems in the evolution of the seed-plant feeding habit by either a micro-organism feeder or a predator: the proteins, including their constituent amino acids, and the sterols.

The quantities of protein, on either a dry or wet weight basis in most Spermatophyta tissues are markedly lower than those of insects and apparently micro-organisms.

Successful synthetic diets normally contain from 25–40 per cent dry weight of protein (Dadd 1963; Chapman 1969). As can be seen from Table 4, many plant tissues are around the lower limit; Boyd (1970) analysed eleven different aquatic plants and found dry weight percentages of protein from 4 to 21, with a mean of 13: much lower values than those of the edible crop plants normally analysed; Russell (1947) gives data for 894 analyses of about 400 different trees and shrubs, the average protein content is only 13·4 per cent of dry weight.

All insects appear to need small quantities of sterols in their diets (Clayton 1970).

Predatory species can utilize the cholesterol and 7-dehydrocholesterol from their food directly in their metabolic processes; phytophagous species have evolved the ability to use a

limited number of plant sterols, probably converting them to cholesterols (Beck & Kapaida 1957; Dadd 1960; Levinson 1962). There appears, however, to be a great deal of specificity; for example, whereas stigmasterol is superior to cholesterol for *Pectinophora* (Vanderzant & Reiser 1956), locusts are unable to utilize stigmasterol and 7-dehydrocholesterol (Dadd 1960, 1963). At least some aphids appear to obtain their sterols from their symbionts (Dadd & Mittler 1966; Auclair 1969); the most frequent and often most abundant sterol in micro-organisms is ergosterol which can be utilized by cockroaches and *Drosophila*, which are scavenging micro-organism feeders (Prosser & Brown 1961).

The ability to utilize the different sterols of animal, microbial or plant origin is clearly a major dietary hurdle to change in feeding habits and Slama (1969) has suggested a further hazard; some of them appear experimentally to act as neurohormone 'mimics'.

However, the value of a diet for growth and reproduction depends not only on the presence and quantities of the various essential components, but even more on the balance between them (Gordon 1959; House 1965, 1969). Many phytophagous insects have adapted to their host plants and their composition over many millions of generations: the optimum amino-acid mixture for the pink bollworm, *Pectinophora gossypiella* (Saunders), corresponds closely to that of cotton protein (Vanderzant 1958). Nevertheless, many problems of balance remain: for most insects methionine, an amino acid relatively scarce in plants (Lord 1968; Boyd 1970) is an essential dietary requirement. The water-soluble B-vitamins, especially thiamine, riboflavin, nicotinic acid, folic acid, pyridoxine, pantothenic acid, inositol, choline and biotin are also essential for insects (House 1958; Dadd 1963; Auclair 1969); plant tissues differ greatly in the quantitative and qualitative representation of these substances (Lord 1968).

The effects of changes in host-plant composition The different parts of plants and of the same plant under different conditions and at different seasons all vary as to their biochemical composition: for example, Weatherley, Peel & Hill (1959) found that the amino-acid composition of the sap in the phloem of willows could vary from 0·5 per cent to 5 per cent. It seems reasonable, therefore, to regard the many changes in insect feeding preference, development rate, fecundity and, indeed, survival associated with changes in the growing conditions of the host plant as evidence that, at many times, diet is far from optimal.

Smith & Northcott (1951) showed that the grasshopper, *Melanoplus mexicanus* (Sauss.) fails to develop normally on wheat if, because of low soil nitrogen, the foliage contains 27 per cent or less of protein. A wide range of phytophagous insects and mites have now been shown to survive better or develop faster or have an increased fecundity on plants with higher N levels (Auclair, Maltais & Cartier 1957; Hukusima 1958; Strickland 1960; House 1961; Soo Hoo & Fraenkel 1966; van Emden, Eastop, Hughes & Way 1969). For some aphids, such responses have recently been linked with sub-optimal levels of only a few amino acids (van Emden & Bashford 1971). The interaction of water-stress and nutritive change and the effect on aphids was pointed out by Kennedy (1958) and has been demonstrated in other aphids by Wearing & van Emden (1967) and Wearing (1967), in thrips by Fennah (1963) and in psyllids by White (1969).

Conversion efficiencies The efficiency of converting food ingested into growth (E.C.I.) is measured by physiologists on a weight basis, whilst ecologists have a very similar measure —the 'ecological' or production consumption efficiency (P/C) which is based on the energy content of the ingested food and the 'production' (growth or biomass produced). When the calorific contents of the food and the animal are similar, as in predators, the values for E.C.I. and P/C will be similar; however, for a phytophagous insect the E.C.I. will be

higher than the P/C, because of the conversion of plant tissues to the higher energy content insect tissue (Morowitz 1968) (Fig. 1; Table 5). Comparisons of these efficiencies for leaf-feeders and predators are given in Table 6; phytophagous species have low efficiencies.

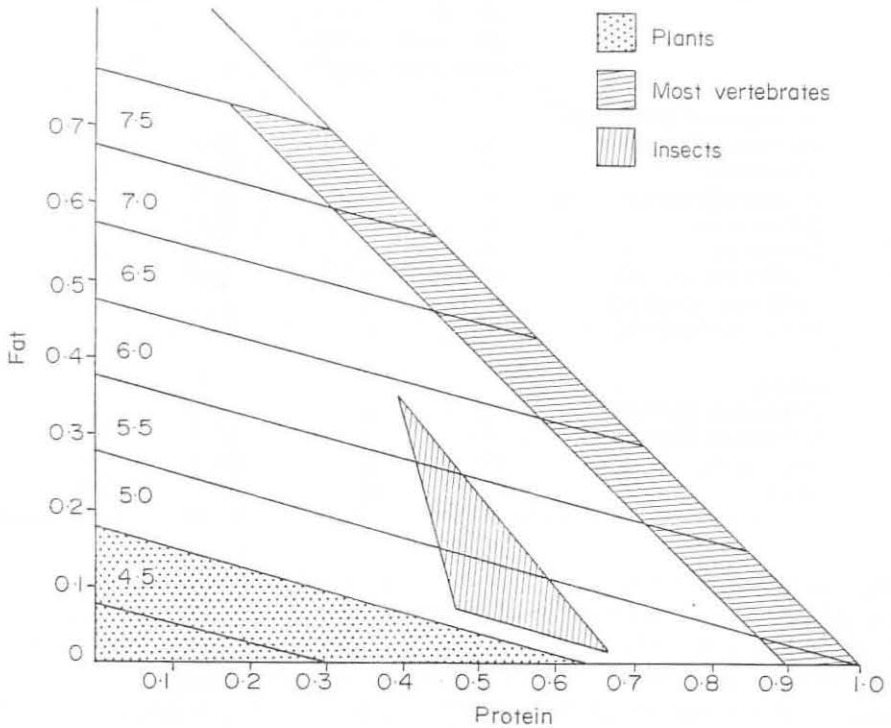

FIG. 1. The relation between composition (fractions of unity dry wt) and energy content (Kcal/gm dry wt) of various groups of living organisms (modified with the addition of insects, from Morowitz 1968)

TABLE 5. Comparison of calorific values of various plant and insect tissues (in Kcal/gm dry wt) (data from Weigert 1964; Cross 1966; McNeill 1971; Boyd 1970)

Plants	
Typha	4·2
Ceratophyllum	3·9
Holcus—seeds	5·8
growing ups	5·4
whole	4·4
Insects	
Tenebrio larva (Col.)	6·6
Pieris larva (Lep.)	5·6
Leptopterna—egg (Het.)	6·3
larva (Het.)	5·8
adult (Het.)	6·0
Philaenus—egg (Hom.)	6·3
larva (Hom.)	5·3
adult (Hom.)	5·8

TABLE 6. Comparison of efficiency of conversion of ingested food (E.C.I.) or the production consumption efficiency P/C per cent (*) in different orders and on different diets (data from Waldbauer 1968; Mukerji & Le Roux 1969*a*, *b*; Gyllenberg 1970; Lawton 1970; Mordue & Hill 1970; McNeill 1971)

	No. of efficiencies determined	No. of different species	Range	Mean E.C.I. or P/C*
Leaf feeders and sap feeders				
Orthoptera (dry wt)	7	2	8–11	9·0
Orthoptera	6	4	10–17	13·4
Phasmida (dry wt)	1	1	8	8·0
Heteroptera	5	1	16–20	17·8
Homoptera	6	1	5–18	13·0*
Lepidoptera (dry wt)	38	9	3–38	20·9
Lepidoptera (fresh wt)	12	9	2–34	19·5
Coleoptera (fresh wt)	1	1	20	20
Predators				
Heteroptera (fresh wt)	2	2	38–51	44·5
Heteroptera (dry wt)	1	1	50	50
Heteroptera	16	1	49	49*
Odonata	1	1	47	47*

Too much emphasis must not be placed on a precise figure because many studies have shown how these efficiencies vary in different habitats, in different seasons and in different developmental stages (Wiegert 1964, 1965; Mordue & Hill 1970; McNeill 1971). These variations do not alter the general conclusion that phytophagous species have lower efficiencies than predators; indeed the seasonal and habitat variations reinforce the point that natural food is often far from ideal.

The conclusion from this consideration of the three types of evidence on the nutritional 'hurdle' is that the foliage of seed plants is, even for those taxa that have evolved the ability to live on it, often only marginally adequate nutritionally: one or more vital constituents may be close to the minimum levels.

Attachment 'hurdle'

Living on the aerial parts of Spermatophyta or the larger Pteridophyta presents problems of attachment that do not occur for insects living on, in or near the soil. This problem can be overcome in two ways:

(a) evolving structural modifications or secreting material to increase the insects ability to 'hold on';

(b) evolving a mode of life so that the insect is cradled by the plant, i.e. leaf-miners, stem-borers and gall formers.

The pre-tarsal structures of many exo- and endopterygote insects (Holway 1935) are assumed to aid in gripping smooth surfaces, although there have been relatively few investigations of their functioning (Gillett & Wigglesworth 1932). The two endopterygote taxa that are particularly successful foliage feeders in the larval stages are the Lepidoptera and Hymenoptera Symphyta. These taxa have evolved, presumably independently, sucker-like abdominal prolegs which bear crotchets in the Lepidoptera. Some Mecoptera and the Zeugloptera, both of which are ground dwellers and considered primitive, also have prolegs but without musculature and crotchets (Chapman 1894; Currie 1932): it seems that the panorpoid orders were pre-adapted in this

respect. Most phytophagous dipterous larvae live in mines, galls or in the soil, but *Cylindrotoma* (Tipulidae) is sometimes found browsing on the leaves of *Arctium* and other low growing plants; it has a number of fleshy appendages on the abdominal segments (Cameron 1918), as do the predatory larvae of Syrphidae and Chamaemyiidae and the planidium type larvae of some tachinids (*Ophirion*) (Clausen 1940). The difficulties of many insects in gripping the smooth lamina of a leaf have perhaps to be observed to be appreciated. Marks' (1970) studies on coccinellid larvae showed how they normally kept to the rim or the veins of a leaf, when the 'edge' could be gripped by the legs on one side. Young coniopterygid larvae will sometimes use the terminal segments of the abdomen to secrete a sticky substance when walking on a leaf (Collyer 1951); their movement almost resembles 'looping'. In at least some chrysomelid larvae, e.g. *Galerucella*, the end of the abdomen is used to aid attachment to the leaf surface during movement. The larvae of many Miridae if suddenly jolted extrude the last part of the rectum which will adhere to the smoothest surface, holding the bug firmly (Southwood & Leston 1959). Many Homoptera are also partly anchored by the rostrum, but this is a delicate structure. Another method is to become attached to the plant, temporarily or more permanently by a secretion, as in aleurodid larvae and scale insects or in mites, spiders, Psocoptera and caterpillars that use silk.

Desiccation 'hurdle'

Although living plant material contains a high proportion of water, there is often a considerable saturation deficit a very small distance from the leaf surface (Ramsay, Butler & Sang 1937) because of air movement. Thus although the active stages of insects can replace moisture by feeding, those that live in exposed situations still need to reduce the desiccation risk; three methods, which are often combined, may be adopted.

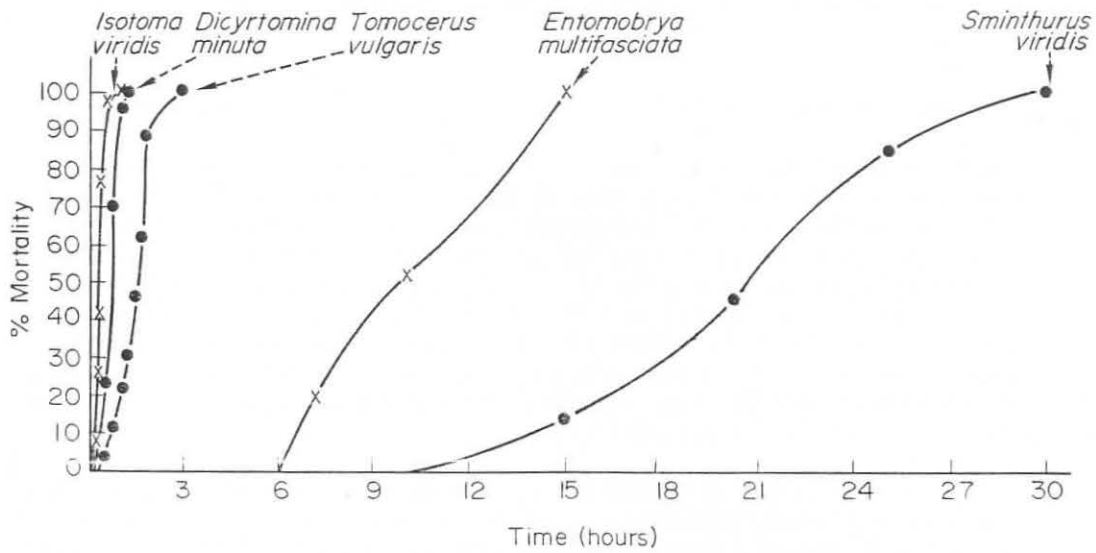

FIG. 2. The mortality rates of various species of Collembola at 50 per cent R.H. (data from Davies 1928*b*)

They may supplement their water intake by 'drinking' free water (Mellanby & French 1958) or they may rest on those parts of the leaf where the boundary layer is deepest (and the humidity highest, as Fennah (1963) found in thrips). Thirdly, and most commonly, water loss is reduced by modifications and development of the cuticle and of the tracheal system (Wigglesworth 1965). Other evolutionary alternatives are to secrete or build a cover that reduces air flow (Psocoptera

and cercopid larvae) or to live in the plant tissue (leaf-miners, gall-insects) or 'plugged-in' to the plants' own water supply (many Homoptera). An interesting case is provided by the Machaerotidae, whose larvae virtually make their own 'ponds' on the host plant; a tube is secreted and then this is filled with the excretory fluid (Evans 1940). Differential resistance to desiccation in relation to habitat is well shown by Davies' (1928*b*) studies on five species of Collembola (Fig. 2). The most resistant species, *Sminthurus viridis* Lubbock, is one of the few Collembola that feeds on seed plants (see below).

The dangers of desiccation are even greater in the non-feeding egg stage with its high surface-to-volume ratio. In many groups this is overcome by the eggs being inserted in plant tissue, but those eggs with long development times need to evolve a method to protect themselves from crushing, enclosure, or suffocation by the surrounding plant tissue. Kershaw (in VAN EMDEN & WAY 1972) has found that eggs of the dipterous leaf-miner *Phytomyza rufipes* Meig. may be 'squeezed' off the leaf by the growth of cells at the point of attachment. The Heteroptera and Lepidoptera are the main orders that lay eggs with relatively long development times and which are exposed on the surface of plants, and within each many modifications have been evolved that serve to reduce water loss (Southwood 1955; Kayumbo 1963; Bartell 1966).

Host finding 'hurdle'

This is a problem for any animal with a discrete food source and it is different only in quality, and not in magnitude, for seed plant feeders in comparison with those arthropods with other feeding habits. Investigations on this aspect have been made by many workers, including Wood (1962) and Kennedy & Moorhouse (1969) and the topic is reviewed here by SCHOONHOVEN (1972) and by WOOD (1972). For seasonal host plants there is also the problem of generation synchrony (COAKER & FINCH 1972).

THE SPERMATOPHYTA-FEEDING GROUPS

Acari Two families, the Tetranychidae and Phytoptidae (Eriophyidae), are well adapted to seed plants (Evans, Sheals & Macfarlane 1961). The former live close to the leaves, often with webbing; some members lay very resistant diapause eggs (Beament 1951). The Phytoptidae live and breed in galls. Many families have scavenging habits, but there is often a general tendency 'to select food of high protein content where this is available' (Hughes 1959) and even the bulb-mite (*Rhizoglyphus echinopus* (Fum. et Robin)) seems to feed only on already injured bulbs (Evans *et al.* 1961). Predatory mites living on plants can survive periods of prey shortage by sucking plant juices (a source of moisture and sugars?), but for development additional protein is required. Normally this is obtained from prey, but pollen grains and fungal spores can serve as substitutes (Evans *et al.* 1961; McMurtry & Scriven 1968).

Collembola The majority of Collembola live in humid conditions and feed on fungi and decaying plant material (Christiansen 1964; Knight & Angel 1967); the latter (wood and humus) is readily accepted when it contains micro-organisms, but not if sterilized (Singh 1969). Many species have been recorded associated with seed plants (Womersley 1939; Paclt 1956), but the feeding of most of these is restricted to pollen grains and/or young seedlings. Both these are rich sources of nutrients, and are without many of the plants' defence mechanisms (see below). Species of *Sminthurus* and *Bourletiella* do, however, feed extensively on the foliage of spermatophytes, particularly Papilionaceae (Fink 1914; Davies 1928*b*, *c*; MacLagan 1932; Folsom 1933; Walters 1968). These plants are relatively high in proteins (Table 4); but phytophagous Collembola also consume pollen grains and fungal spores (Christiansen 1964; Walters 1968; Kevan &

Kevan 1970). *Sminthurus viridis* Lubbock is more resistant to desiccation than many other Collembola (Fig. 2), nevertheless it thrives best on leaves close to the soil and lays its eggs in damp soil (Davidson 1934). Thus the Collembola are particularly interesting as representing a group that has almost, but not quite, overcome the 'hurdles' for the exploitation of the Spermatophyta for living and feeding.

Orthoptera The sub-order Ensifera, containing Gryllacridoidea, Tettigonioidea and Grylloidea, exhibits a range of feeding habits: decaying plant and animal matter, living invertebrates and plant tissue. Most frequently the species are mixed feeders, living on or close to the ground, and the plants attacked are seedlings, e.g. *Daihinia brevipes* Haldeman studied by Whitehead & Miner (1944). However, the Gryllacrididae and many Tettigoniidae live on trees; the former are almost entirely predacious and construct shelters from rolled leaves (Imms 1957). Tettigoniidae lay their eggs in plant tissues. In the suborder Caelifera, the Tetrigidae and Tridactylidae feed mostly on algae, but the Acridoidea are entirely adapted to feeding on the Spermatophyta: the significance of this evolutionary breakthrough is evinced by the number of species—10,000, which is more than the total of all the other orthopteran superfamilies—and the abundance of many grasshoppers and locusts. The Acridoidea have six gastric caeca, whilst Ensifera have two; but functional studies do not seem to have been made to determine whether the ability to develop on a diet solely of plant material is related to this structural difference. The nutritional requirements of acridids are similar to those of most phytophagous species apart from the need for lipogenic factors, choline and inositol (Dadd 1963). However, the Acridoidea are not as well adapted to life on seed plants as are some other groups of insects; their efficiency of conversion of ingested food is low (Table 4) and they nearly always have to return to the soil for egg laying.

Phasmida This order is entirely phytophagous: most species feed on trees. In the one species where nutritional studies have been made the efficiency of conversion is similar to that of Orthoptera (Table 5). The eggs fall to the ground and the young larvae commence life by finding and ascending the host tree. Not surprisingly mortality is high (Readshaw 1965).

Thysanoptera Grinfel (1959) has suggested that thrips were originally pollen feeders and that the asymmetrical mouthparts were evolved to facilitate the extraction of the contents of pollen grains. The majority of species still frequent flowers and augment their diet with pollen grains; some are predacious and some feed on debris and fungi. Phytophagous thrips mostly feed on those parts of the plant particularly rich in proteins and sterols: young growth and reproductive organs. Fennah (1963) found that *Selenothrips rubrocinctus* (Giard) flourished best on water-stressed cashew trees when the amino-acid content of the sap was higher. Thus, although there have not been any studies on the nutritional requirements of Thysanoptera, it would seem that they require higher levels of amino acids in their diet than many other phytophagous groups. Shoots and young leaves attacked by thrips often become curled and distorted. These incipient galls provide shelter. *Kladothrips* and some other genera are true gall-formers (Mound 1971). The Terebrantia lay their eggs in plant tissue.

Hemiptera This large order contains many phytophagous species: the 'sucking' mouthparts preclude the ingestion of solid food (except perhaps in the Corixidae) and so the diet is restricted to plant sap or sap plus externally digested solid material. Plant sap is usually low in amino nitrogen and, in general, the Hemiptera have overcome this either by increasing the 'throughput' (Homoptera) or by being selective in their feeding sites (Heteroptera). On the other hand the structure of the hemipterous mouthparts has the potential advantage of allowing selective feeding within the plant, not only selection of the tissue, but selection of all contents without the cellulose walls. The Homoptera are entirely plant feeding: the annectant Peloridiidae live in humid situations (amongst bryophytes, which apparently provide their food) and the gut has no filter

chamber (Pendergrast 1962). Their nutrition would warrant investigation—a low intake (because they neither have a filter chamber nor are turgid like some aphids) of bryophyte sap would seem an unpromising diet. The majority of Homoptera feed on the sap of seed plants, but a few are fungus feeders and the Typhlocybinae and some Sternorrhyncha are believed to extract the contents of mesophyll cells. Most sap feeders obtain this from the phloem vessels of the plant, here the sap is under positive pressure so that the pharyngeal muscles must serve more as a constricting 'tap' than a pump. Cercopidae are considered to feed from the xylem (Wiegert 1964) where the sap is under negative pressure; the dynamics of this have not been elucidated. The filter-chamber of the gut is considered to aid the throughput of sap and prevent dilution of the blood by water absorbed from the gut by osmosis. Exceptionally in the aphids, only the Lachnidae and some Aphididae have a filter-chamber; Goodchild (1966) suggests that the other aphids have evolved a special method of avoiding the excessive dilution of the blood by the maintenance of internal turgor pressure.

Most Homoptera (the Typhlocybinae are an exception) have symbiotic micro-organisms which are generally confined to mycetomes, and are passed on through the eggs (Buchner 1953). Aphids die if their symbionts are killed with antibiotics (Ehrhardt 1968): studies with synthetic diets show that aphids are exceptional in insects in not requiring dietary sterols, and it seems likely that the symbionts provide these (Dadd & Mittler 1966; Dadd & Krieger 1967). The Homoptera are rivalled only by the Lepidoptera in their total adoption of seed-plants for food and shelter. Modifications of the gut and the possession of symbionts have enabled them to overcome the dietary 'hurdle', whilst the almost continuous feeding of many larvae provides both abundant moisture to help overcome desiccation and another means of attachment. Some larvae are covered in froth (Cercopidae), abundant flocculent wax (some Fulgoroidea, Psyllidae and Aleyrodoidea) or build liquid-filled tubes (Machaerotidae). Many Psyllidae are covered by elaborate cases or 'lerps' and many Coccoidea with a variety of waxy and other secretions. Many such secretions are usually considered to help prevent desiccation, but they may also provide some protection against natural enemies and against dislodgement, as do the galls formed by some Aphidoidea, Coccoidea and Psylloidea. Egg desiccation is avoided by insertion into plant tissue in Auchenorrhyncha and Psylloidea, by protection by the female in Coccoidea and by viviparity in many Aphidoidea. Exposed eggs are laid by Aleyrodidae and some Aphidoidea.

The Heteroptera were undoubtedly originally predacious or perhaps fungivorous. Plant (Spermatophyta) feeding has evolved independently several times in the suborder, but the bugs are always selective in their feeding sites—flower buds, the growing tips of shoots, young or ripe fruits or seeds, parts that are particularly rich in proteins and other nutrients and high in energy (Tables 4, 5). By being selective the Heteroptera can compensate for their small intake of food, compared with the Homoptera. The stylet tips of many Heteroptera move round in the plant tissue and enzymes are inserted with the saliva (Nuorteva 1956, 1958, 1962; Miles 1969); their pabulum may therefore contain substances other than those commonly found in sap, or at least a different balance of substances. Plant-feeding Heteroptera will probe many parts of the plant (and humans!) for water, but for development access to meristematic areas or arthropod food (in many Miridae which are partial predators) is essential. Some Tingitidae, a family which includes some bryophyte feeders and the only gall-formers in the Heteroptera (Drake 1957; Monod & Carayon 1958), and some little known shield bugs, Phloeidae (Leston 1953), are possible exceptions. Symbionts in gastric caeca or mycetomes are found in all phytophagous Pentatomoidea (but are absent in the predatory Amyoteinae), in most phytophagous Coreoidea (the exceptions seem to feed on Papilionaceae) and in many of the seed-feeding Lygaeoidea. The eggs of the more primitive phytophagous families, notably the Pyrrhocoridae and Cydnidae, are not well waterproofed and are laid in the soil. Many cydnids are subterranean but in some Sehirinae, like Pyrrhocoridae, the females leave the hosts and move into the soil for oviposition and the young larvae move back up the plant. The eggs of the Pentatomidae, Coreoidea and higher Reduviidae (which are predators) which are laid in exposed situations on plants have elaborate structural modifications (Southwood 1956; Cobben 1968) which appear to reduce water loss (Kayumbo

1963). Tingidae, Miridae and the predatory Cimicoidea that live on seed plants lay their eggs in plant tissue (Johnson 1934; Kullenberg 1946) and may absorb water from the plant (Johnson 1937).

Lepidoptera The larvae of the great majority of the 100,000 species feed on seed plants, but those of the most archaic suborder, Zeugloptera, are moss or detritus feeders (Chapman 1894) and they live in a humid environment, as do the larvae of the suborders Dachnonypha and Monotrysia, which are root feeders or leaf miners. Only the larvae of the 'highest' suborder (Ditrysia) feed on the surface of their host plants. Their efficiencies of conversion of ingested food, on their preferred host plants, are often high (Table 6) (Soo Hoo & Fraenkel 1966; Waldbauer 1968) and, unlike the Diptera and many other orders, the adults take little or no food since the nutritional requirements of the whole generation are met by the larva. Lepidoptera are therefore extremely well adapted to feeding and living on seed plants, so much so that the secondarily ectoparasitic Cyclotornidae and Epipyropidae and the occasional predator elsewhere (especially in the Lycaenidae), habits common in most other orders, are surprising exceptions. The archaic suborders do however, as shown above, reveal some of the evolutionary steps towards this overwhelming success.

Diptera In spite of their high evolutionary status in many respects, few Diptera obtain their nutrition entirely by browsing *externally* on plant (Spermatophyta) material. The larvae of Cylindrotomini (Tipulidae) feed on the foliage of aquatic and low-growing plants (Cameron 1918), and those of *Mesograpta polita* (Say) (Syrphidae) feed on maize pollen; these are among the very few examples. The great majority of families are scavenging micro-organism feeders. In several (Tipulidae, Bibionidae, Syrphidae, Psilidae and Anthomyiidae) the larvae live in the soil and attack the roots or bulbs of plants. The studies of Friend *et al.* (1959) on *Hylemyia* (Anthomyiidae) show that in this species bacterial infection of the food (perhaps brought about by the feeding activities of the larvae) is essential. In the Chloropidae a range of larval feeding habits occurs which includes parasites of vertebrates and insects as well as plant shoot-borers that exhibit an interesting gradation from species that attack only already diseased or decaying shoots (e.g. *Elachiptera*) through those that live in previously healthy plant tissue (*Oscinella*) to formers of rudimentary galls (*Chlorops*). The leaf or stem-mining, or gall-forming Agromyzidae, also the leaf miners and gall makers amongst the Cecidomyiidae, Trypetidae and Anthomyiidae, feed on a wide range of Spermatophyta. Agromyzidae and Trypetidae are the only families of Diptera entirely dependent on the aerial parts of seed plants for food; Spencer (1971) has shown an interesting co-evolutionary relationship between Agromyzidae and Spermatophyta. The nutritional requirements of these flies have not been investigated, nor the rôle of the bacteria and other organisms that often live in the mines and galls. *Fergusonia nicholsoni* Tonn, an agromyzid (sometimes placed in a distinct family), lives symbiotically with nematodes in its galls; the nematodes provide the stimulus for the gall formation (Currie 1937). Many dipterous larvae are predacious and those of some Syrphidae, Chamaemyiidae and some Cecidomyiidae, together with the 'planidium' first stage larva of certain Tachinidae, are the principal dipterous larvae found living externally *on* plants. Gordon (1959), Sang (1959) and others have emphasized the importance of the nutritional status of the egg in influencing the dietary requirements for development. Indeed nutritional intake needs to be viewed on a generation basis and in Diptera, feeding by the highly mobile and highly sensorily perceptive adult is not only relatively important, but often essential for egg production (Harlow 1956; Christophers 1960): many feed on pollen and nectar from flowers, acting at the same time as pollinating agents and establishing another, often elaborate (as in *Arum maculatum*), link with plants. Coaker & Finch (1972) discuss this for the cabbage rootfly.

Hymenoptera It could be claimed that some of the most elaborately evolved plant/insect relations are found in this, the most species-prolific of all orders. The suborder Symphyta parallels

the Lepidoptera, admittedly rather less successfully, as external feeders on plant foliage, mainly on ammophilous plants and ferns (Benson 1950). The more primitive Pamphiliidae lay their eggs externally on leaves, but the Cephoidea and Tenthredinoidea oviposit in plant tissues. Tenthredinoid eggs are accompanied by a secretion from the female accessory gland that is presumed to protect them from the rotting or growth of the surrounding tissue. In the suborder Apocrita, the bees have become secondarily dependent on plants for their diet, and their rôle as pollinators is so vital to plants that remarkable co-evolution has occurred (Leppik 1957; Yeo 1972). Some ants have achieved extraordinary symbiotic relationships with plants, as exemplified in the symbiotic relationship between the acacia thorn ants and the acacia (see above). Many adult 'Parasitica' feed on nectar and pollen from flowers (Leius 1960) much in the manner of adult Diptera, but the elaborate relationships in this group of superfamilies occur in the Cynipoidea, where most species are gall formers as larvae and in the Chalcidoidea, where gall formation by the larvae is generally simpler and they often live in seeds. The Agaonidae or fig insects perhaps represent the most extreme case of symbiosis between an insect and a plant (Hill 1967, 1971); this is discussed below. From the point of view of co-evolution the host relations of the Cynipidae are intriguing; 86 per cent of the world species of gall formers are attached to *Quercus*, 7 per cent to *Rosa* and the remaining 7 per cent mostly to Compositae (Kinsey 1920). The biochemical basis for this bias has not been determined. Malyshev (1966), in a detailed discussion of the evolution of the Hymenoptera, suggests that since *Panorpa* will feed on pollen, primitive Xyelidae or their ancestors may have commenced by feeding on gymnosperm pollen on the ground and subsequently, as in the present-day species, have come to feed on the pollen cones on the trees themselves. It has been noted above (p. 7) that pollen has a high protein content relative to many plant tissues. It is noteworthy that those Pamphiliidae genera attached to gymnosperms are more primitive than those on angiosperms (Benson 1945).

Coleoptera Although Britton (1970) states that most 'Coleoptera are phytophagous', relatively few groups are able to live externally on plants as larvae on a diet of foliage: these are principally the Chrysomelidae, and some Curculionoidea, whilst Scarabaeidae do as adults. Many others feed on the roots of plants, in the wood or seeds, or in decaying plant material. In general, Coleoptera resemble Diptera in really being mainly scavenging micro-organism feeders as larvae: those feeding on wood have internal symbionts (Brooks 1963), or, in the case of 'ambrosia beetles', an external symbiosis with certain fungi (Baker 1963). The association with dead or dying as opposed to living plant tissue is underlined in the Attelabidae where the female cuts and rolls the leaf or rings the shoot after oviposition so that it withers and normally falls to the ground. A study of the nutritional requirements of these larvae, of the nutrients available in the cut and uncut leaves, and of the related strictly phytophagous Curculionidae would be of evolutionary interest.

The plants' evolutionary reactions to insect attack

The success of insects in the biological control of weeds is dramatic evidence of the impact of insects feeding on seed plant populations (Holloway 1964; Harris 1972). Their effects on natural vegetation are seldom assessed, again apart from the more dramatic cases of defoliation that may eventually lead to the death of the tree (Henson & Stark 1959; Churchill, John, Duneon & Hodson 1964).

In spite of the large number of propagules produced by plants the rôle of insects in the evolution and ecology of plants through their effects on seeds and young seedlings may be very significant (Breedlove & Ehrlich 1968; Janzen 1969, 1971). Furthermore the relationships we now observe are based on up to 200,000 million years of co-evolution, but even today when a phytophagous species first attacks a new host it often inflicts disproportionately heavy damage. Good examples of this are provided by *Lepidosaphes newsteadi*

(Sulz.) which was introduced into Bermuda around 1940 and became attached to the endemic conifer *Juniperus bermudiana* L., which was almost exterminated (Thompson 1954; Bennett & Hughes 1959) and by the mite, *Phyllocoptes destructor* Keifer, on tomatoes in California (Bailey & Keifer 1943).

It is therefore not surprising that in the course of evolution seed plants (and some of the cryptogams) have developed mechanisms for resistance to insect attack (Painter 1951). These defences are numerous and undoubtedly include developmental ones, such as the germination of seeds in early spring in temperate climates. However, the majority can be classified as physical or chemical (Stahl 1888).

Physical For many insects a thickened plant cuticle prevents or reduces feeding (Ripley & van Heerden 1939; Tanton 1962; Agarwal 1969; Feeny 1970). Its rôle is particularly important for small insects, including the early instars of relatively large species (Bernays & Chapman 1970). The cuticle of leaves thickens as they mature (Martin & Juniper 1970). Plants often have hairs and spines on their epidermis: in cotton long hairs on the leaf confer resistance to the leafhopper, *Empoasca lybica* (de B.) (Pearson 1958), and in the grass *Holcus* deter feeding by early instars of *Chorthippus* (Bernays & Chapman 1970). Johnson (1953) showed that the hooked hairs on *Phaseolus vulgaris* L. would trap, and so kill, *Aphis craccivora* Koch: the hairs on the leaves were most dense on the growing shoot—a portion of the plant nutritionally favourable for insects (p. 9) and with a thin cuticle.

Many plants possess glandular hairs: these too will trap small, weak insects (Johnson 1956). It is interesting that a tribe of Mirid bugs, the Dicyphini, seem largely confined to plants with these types of hairs, probably using the entrapped insects as a small but vital secondary source of nutrition, whilst members of the genera *Cyrtopeltis* and *Setocornis* live on sundews (*Drosera*) and *Byblis* in Australia and feed on the trapped insects (China 1953; Russell 1953). The cuticular teeth of holly make it resistant to the oligophagous oak eggar moth larva, *Lasiocampa quercus* (L.) (Merz 1959). The resins of conifers often cause the death of invading insects (Stark 1965). Harris (1960) found that some third instar larvae of the pine shoot moth, *Rhyacionia buoliana* (Schiff.) were drowned in the resin flow as they invaded the buds of young trees and he suggested that the low rate of infestation of mature stands is due to the resting buds developing adequate resin defences earlier. The high silica content of some plants and crystalline materials in the leaves may confer resistance by acting as barriers to feeding (Merz 1959; Pathak 1969).

Chemical Plants contain a large number of so-called secondary substances, including alkaloids, betaines, glycosides, tannins, flavenoids, essential oils, saponins and organic acids. Fraenkel (1953, 1959, 1969) and Lipke & Fraenkel (1956) have advanced the view (which Fraenkel points out was originally propounded by Stahl 1888) that these compounds have been evolved as defence mechanisms against insects, pathogens and perhaps competitors. This view has been supported, so far as insects are concerned, by Dethier (1954, 1970), Thorsteinson (1960), Ehrlich & Raven (1965), Jermy (1966), Matolcsy, Saringer, Gaborjanyi & Jermy (1968) and Levin (1971). Jermy (1966) showed, for several plant feeding species, that non-host plants contain feeding deterrents. Much of the interaction between insects and these secondary plant substances is sensory, and such substances can inhibit feeding (Thorsteinson 1960; Haskell & Mordue 1969; Ishikawa, Hirao & Arai 1969; Gill & Lewis 1971). Occasionally insects will feed on plants that prove toxic to them; a member of the *Aphis fabae* Scop. group that normally lives on *Tropaeolum* dies if it feeds on *Vicia faba* L. (Taylor 1959). The hairs of plants may secrete substances that kill insects that come in contact with them; Thurston, Smith & Cooper (1966) showed that the hairs of *Nicotiana* secrete alkaloids, especially nicotine, that kill aphids. Pyrethrin, derris and rhyania are other plant products whose insecticidal properties are well known.

Very recently it has been found that some plants synthesize and accumulate sterols closely related to the insect hormone, ecdysone. These phyto-ecdysones have been found in fifteen

families of Spermatophyta and three families of fern (Imai, Toyosato, Fujioka, Sakai & Sato 1968; Williams 1970). Other studies revealed that various gymnosperms contain materials which, with Pyrrhocoridae, exhibit activity similar to that of the juvenile hormone; these have been called juvabione (methyl todomatuate) and dehydrojuvabione (Slama 1969; Williams 1970). Most recently insect sex-pheromone mimics have been found in four families of plants, Compositae, Labiatae, Araliaceae and Simaroubaceae (Bowers & Bodenstein 1971).

These 'special chemicals' are not the only means that plants can evolve to protect themselves from insect attack; it has been pointed out above that insects face certain nutritional problems living on plants. Plant proteins are often deficient in some of the amino acids essential for insects; tryptophane and methionine are particularly scarce (Lord 1968; Boyd 1970). As Gordon (1959) has suggested these deficiencies 'may be a result of natural selection for inedibility'. Moreover high consumption of some so-called nutrients (e.g. amino acids) may reduce the growth of aphids on plants (van Emden & Bashford 1971). The interaction between the nutritive value of the plant and secondary plant substances has been demonstrated by Feeny (1968, 1969, 1970) and Feeny & Bostock (1968) for the oak and its tannins. During the growth season the protein content of the leaves falls and the tannin content rises; the two interact to bring about a marked and accelerating fall in the nutritive value of oak leaves, because tannins combine with proteins to form relatively indigestible complexes. Feeny (1970) concludes by describing tannins as 'broad spectrum defensive mechanisms', having repellent, antibiotic and growth inhibiting properties, the latter arising from their influence on protein availability.

The insects' evolutionary response to plants' defence mechanisms

The pattern of insect/plant associations

As plants have a range of defence mechanisms, often including chemicals with insecticidal properties, it is reasonable to seek parallels between insects' resistance to pesticides and

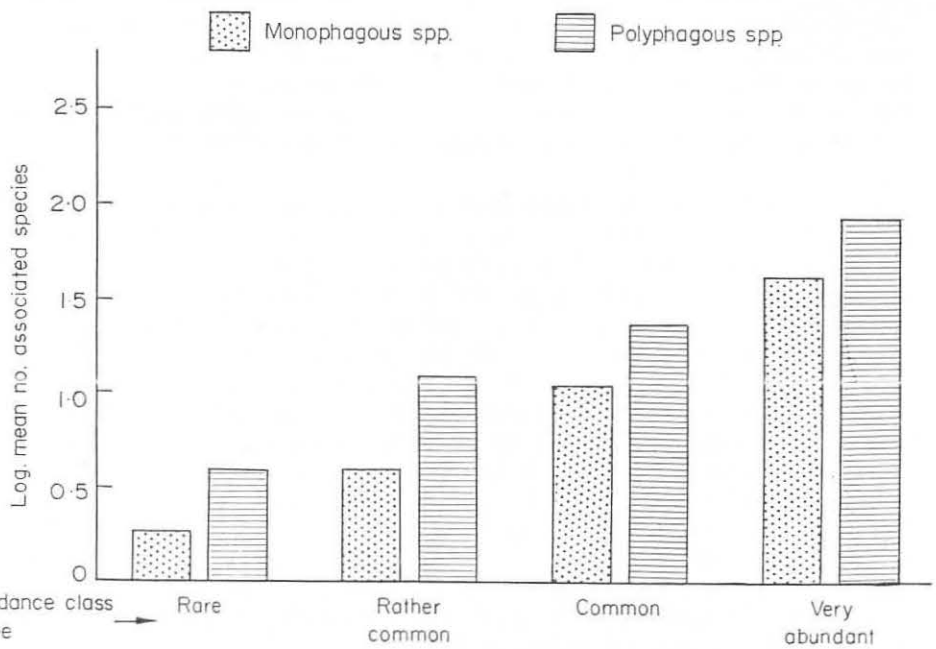

FIG. 3. The mean numbers of species of insects associated with Hawaiian trees of different abundance categories (data from Southwood 1960)

insects' resistance to plants (Painter 1951; Southwood 1961*b*; Dethier 1970): the latter condition is normally referred to as an insect/plant association. The more widely and frequently an insecticide is used, the more insects will normally become resistant to it. The rôle of frequency of exposure of the pattern of insect/plant associations is best observed among different species of trees, which are plants of comparable size present in the field continuously for long periods. The different species of trees are thus more directly comparable than different species of herbs. Numerical analyses have been made for British and Hawaiian trees and their associated insects (Figs 3, 4), whilst comparison has been made of the insect fauna of the same species of tree in Britain, Europe, Russia, Sweden and Cyprus (Southwood 1960, 1961*a*). These data all show that the number of species of

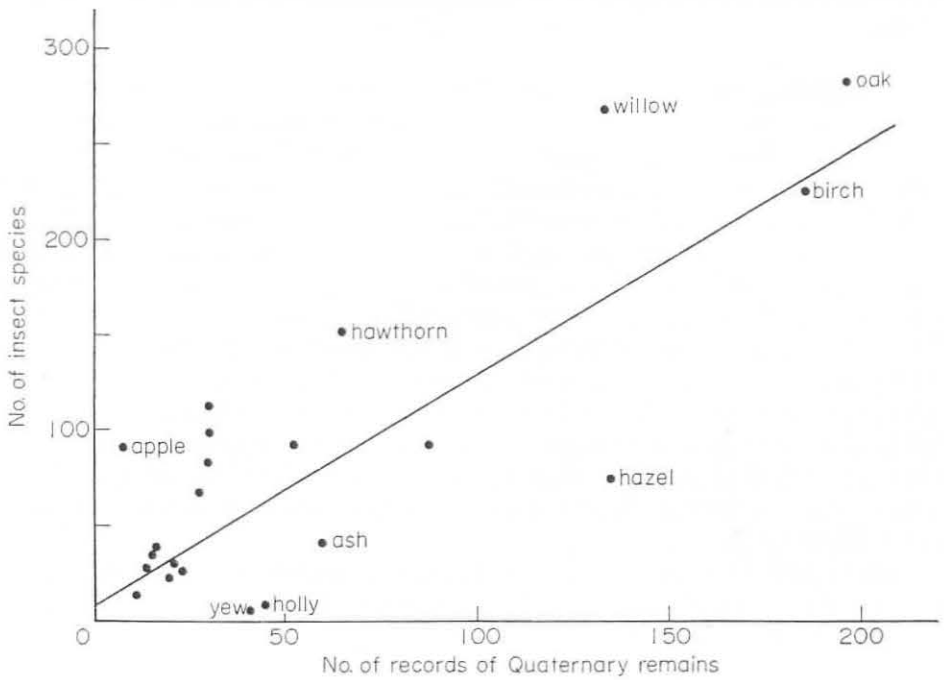

FIG. 4. The relationship between the number of species associated with a tree and its abundance in recent geological times (after Southwood 1961*a*)

insect associated with a tree is proportional to the tree's recent abundance. This conclusion has also been confirmed with Homoptera in Australia (Evans 1966). When trees are widely planted, new species of insect often adapt to them, e.g. the *Salix* feeding mirids. *Plesiocoris rugicollis* (Fall.) and *Orthotylus marginalis* Reut. have, in this century, developed the ability to live on apple (*Malus*). The chances of transfer will be affected not only by tree abundance, and by seasonal and other factors, but also by the insects' 'degree of predilection' (Southwood 1961*b*) for change to the new host, which is a reflection of the biochemistries of the previous and new host, as well as of the metabolism of the insect: a phenomenon analagous to cross-resistance to insecticides. Frequently the degree of predilection is a reflection of the botanical affinity of the new with the present host plant (as with *Malus* and *Crataegus*), or is explicable in terms of the anomalous distribution of secondary plant substances (Dethier 1954; Ehrlich & Raven 1965). Some examples, such

as the predilection of *Salix* insects for Rosaceae, especially *Malus* (Benson 1945; Hering 1951; Southwood 1961*b*), are still unexplained.

When the insect abundance/host tree relationship is determined for an area (Fig. 4) it is found that certain trees have more associated species than normal and others have fewer: these resistant species are interesting as they must have defence mechanisms that are particularly difficult for insects to overcome. In Britain three resistant trees are *Fraxinus* (Oleaceae), *Ilex* (Aquifoliaceae) and *Taxus* (Taxaceae) and in Hawaii *Osmanthus* (Oleaceae) and another *Ilex* species (Southwood 1961*b*). The biochemistry of the Oleaceae and Aquifoliaceae does not seem to have been investigated from this point of view; in the latter family it could be a physical resistance. Phyto-ecdysones have recently been shown to be widely distributed in Taxaceae, and to be present in all members of the genus *Taxus* that were tested (Williams 1970); the leaves, shoots and seeds also contain the alkaloid taxine.

The utilization of secondary plant substances by insects

When insects become resistant to secondary plant substances they frequently, to use a slightly misleading colloquial analogy, become 'hooked' on them. Several of these secondary plant substances have been found to provide tokens for host-plant recognition or for feeding, sometimes acting on their own, sometimes synergestically with nutrients (Thorsteinson 1960; Dethier 1966, 1970; Fraenkel 1969; Hsiao 1969; Ishikawa *et al.* 1969; Ma 1969; Rees 1969). Indeed as Kennedy & Booth (1951) and Kennedy (1953) pointed out, insects are likely to use more than one substance to discriminate between plants, and the use of secondary plant substances in this respect is clearly of evolutionary value. Individual receptors have been identified (Dethier & Schoonhoven 1969; Schoonhoven 1969*a*, *b*) and plant recognition by lepidopterous larvae is reviewed by Schoonhoven (1972). Host plant recognition is, of course, often equally or even more important for the ovipositing female (Yamamoto, Jenkins & McClusky 1969) and the presence of the host plant can have a marked effect on the female's reproductive processes (Labeyrie 1962, 1970; Hillyer 1965).

Insects have gone further than simply using secondary plant substances as token stimuli, they may utilize these substances in their own defence mechanisms (Eisner 1970; Rothschild 1972).

The evolving relationship—predatory, parasitic or symbiotic?

The insect/plant relationship in all its diversity has been evolving for hundreds of millions of years and, as the development of new pests and host plant associations shows, is still evolving. Gordon (1959) refers to 'an unending biochemical contest between metazoan and the food organism' and Dethier (1970) emphasizes that the relationship 'arose as a consequence of the interaction of two independently mutating systems'. The mutations are, of course, independent, but ecologically the two biochemical systems are interlinked and, as is frequent in the evolution of interactions between organisms, contest evolves to compromise. In the insect/plant relationship the full spectrum from plant predator via plant parasite to symbiont can be observed.

Heteroptera are frequently plant predators: they select parts of the plant with high meristematic activity, which have a high nutritive value, and in the only species studied, the conversion efficiency is high (Table 4) (McNeill 1971). Because of the parts of the plant they select, their feeding method and the enzymes they inject (Nuorteva 1954, 1955,

1956; Miles 1969), small numbers of bugs often have a large impact on the plant, i.e. they are low density pests (e.g. *Pseudotheraptlus wayi* Brown (Way 1953*a*) and *Distantiella theobroma* (Distant) (Johnson 1962; Leston 1970)). Many are plant predators in the true sense that they kill individual plants, seedlings or particularly seeds: Rhyparochrominae carry seeds in their raptorial forelegs.

The Homoptera, particularly the aphids, provide examples of highly evolved plant parasites: they can occur in considerable numbers on a single host and, as Way (1968) has shown, they have intraspecific mechanisms that normally prevent their populations rising to levels that will prematurely destroy the host plant (VAN EMDEN & WAY 1972). A group of aphids becomes intimately involved with the physiology of the host plant: they respond to changes in the composition of the host (Dixon 1970) and they can influence the flow of nutrients within the plant, acting as a 'sink' (Kennedy 1958; Way 1968; KENNEDY & FOSBROOKE 1972).

The interactions between the insect parasite and its host plant often involve (directly or indirectly) plant growth hormones and similar substances (OSBORNE 1972). The Hemiptera secrete polyphenol oxidase in the saliva: Miles (1968*b*, 1969) suggests that this is primarily a detoxifying agent, but that it will have the effect of allowing the accumulation of indol-3-yl-acetic acid in adjacent cells and hence the onset of gall formation. The mechanism of gall formation, with the remarkable host specificity by the insect and characteristic, often insect specific response by the plant, is not yet elucidated. Sometimes insects seem able to secrete plant growth substances (Miles 1968*a*, *b*). Cecidomyiidae seem to re-secrete the plants' own hormones and promote a wound reaction (Dieleman 1969), whilst in the Hymenoptera nucleic acids may be involved (Went 1970). The growth and differentiation system of plants involves a number of different biochemical systems, and different insect groups may differ as to which of these systems they modify to induce galling.

The relationship between the gall former and its host plant is very intimate and in the fig-insects, Agaonidae, has reached the level of symbiosis. The young larvae live in special gall flowers of the figs; male and sometimes normal female flowers also occur in the same receptacle ('the fig'). After pairing with females and enlarging, with their mandibles, the entrance to the fig, the apterous males die but the winged females leave with fig pollen in a special sac or leg pocket. In their search for an oviposition site they carry this pollen to other flowers. They can only oviposit successfully in 'gall flowers': here oviposition stimulates development of the endosperm (Grandi 1929; Hill 1967, 1971; Ramirez 1969, 1970).

Further evidence of the closeness of the insect/plant relationship may be seen in the direct phenotypic effects plants may have on the insects living on them (Southwood & Blackith 1960; Mound, 1963; Mittler & Sutherland 1969) and in the taxonomic co-evolution that sometimes occurs between groups of insects and plants (Ehrlich & Raven 1965; Spencer 1971). However, the association between insect and plant taxa may often be due to insects having a predilection for change to plants closely allied to their hosts (see above, also EASTOP 1972).

In conclusion, it can be seen that the evolutionary path of the phytophagous insect has not been an easy one; pollen feeding often seems to represent 'the first step' and feeding in or on foliage 'full success'. Relatively few orders have achieved this, although those that have, have reaped a rich reward, both in number of species and often in abundance of individuals. Plants have responded to insect attack and thus insects and plants must be viewed as two co-evolving, competing and often mutually dependent biochemical systems: the balance between them is often very fine and so relatively small biochemical changes may have large ecological effects.

I am greatly indebted to many colleagues for valuable criticisms and advice on specific points: those that have helped me include H.F.van Emden, H.E.Goto, J.S.Kennedy, T.Lewis, S.McNeill, O.W.Richards and H.Ross.

DISCUSSION

Dr W.D.Ryder: Your reference to ants protecting their acacia host trees against fire suggests you were not excluding human influences on the insect/plant relationship. Bearing in mind your comment on the very minor rôle of plants in the transportation of insects, would it not be true to say that the relatively modern development of human transportation has greatly affected the transportation of insects on plants?

Professor Southwood: You are perfectly correct; but I think this is *indirect* transportation on the part of the plant, because after all the plant has been transported by man. But it has indeed had very significant effects on the insect/plant relationship; movement of crops and of insects around the world is a topic which I didn't touch on and I am glad you have raised it.

REFERENCES

AGARWAL, R.A. (1969). Morphological characteristics of sugar cane and insect resistance. *Entomologia exp. appl.*, **12** : 767–776.

AUCLAIR, J.L. (1969). Nutrition of plant-sucking insects on chemically defined diets. *Entomologia exp. appl.*, **12** : 623–641.

AUCLAIR, J.L., MALTAIS, J.B. & CARTIER, J.J. (1957). Factors in resistance of peas to the pea aphid, *Acyrthosiphon pisum* (Harr.) (Homoptera : Aphidae). II. Amino acids. *Can. Ent.*, **89** : 457–464.

BAILEY, S.F. & KEIFER, H.H. (1943). The tomato russet mite, *Phyllocoptes destructor* Keifer: its present status. *J. econ. Ent.*, **36** : 706–712.

BAKER, J.M. (1963). Ambrosia beetles and their fungi, with particular reference to *Platypus cylindrus* Fab. *Symp. Soc. gen. Microbiol.*, **13** : 232–265.

BARTELL, R.J. (1966). *Studies on water loss from the eggs of Lepidoptera.* Ph.D. thesis, University of London.

BEAMENT, J.W.L. (1951). The structure and formation of the egg of the fruit tree red spider mite, *Metatetranychus ulmi* Koch. *Ann. appl. Biol.*, **38** : 1–24.

BECK, S.D. & KAPAIDA, G.G. (1957). Insect nutrition and metabolism of sterols. *Science, N.Y.*, **126** : 258–259.

BECK, S.D., LILLY, J.H. & STAUFFER, J.F. (1949). Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.). I. Development of a satisfactory purified diet for larval growth. *Ann. ent. Soc. Am.*, **42** : 483–496.

BENNETT, F. D. & HUGHES, I.W. (1959). Biological control of insect pests in Bermuda. *Bull. ent. Res.*, **50** : 423–436.

BENSON, R.B. (1945). Classification of the Pamphiliidae (Hymenoptera Symphyta). *Proc. R. ent. Soc. Lond.*, **14** : 25–33.

BENSON, R.B. (1950). An introduction to the natural history of British sawfly. *Trans. Soc. Br. Ent.*, **10** : 45–142.

BERNAYS, E.A. & CHAPMAN, R.F. (1970). Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera : Acrididae) in the field. *J. Anim. Ecol.*, **39** : 761–776.

BOWERS, W.S. & BODENSTEIN, W.G. (1971). Sex pheromone mimics of the American cockroach. *Nature, Lond.*, **232** : 259–261.

BOYD, C.E. (1970). Amino acid, protein and caloric content of vascular aquatic macrophytes. *Ecology*, **51** : 902–906.

BREEDLOVE, D.E. & EHRLICH, P.R. (1968). Plant herbivore co-evolution: lupines and lycaenids. *Science, N.Y.*, **162** : 671–672.

BRITTON, E.B. (1970). A review of *Homolotropus* Maclean (Col., Scarabaeidae, Melolonthinae). *J. Aust. ent. Soc.*, 9 : 42–48.

BROOKS, M. A. (1963). The micro-organisms of healthy insects. In Steinhaus, E.A. (ed.) *Insect pathology —an advanced treatise*, 1 : 215–250. Academic Press, New York & London.

BUCHNER, P. (1965). *Endosymbiosis of animals with plant micro-organisms* (translated by B. Mueller). John Wiley & Sons, New York, London & Sydney, 909 pp.

CAMERON, A.E. (1918). Life-history of the leaf-eating crane-fly, *Cylindrotoma splendens* Doane. *Ann. ent. Soc. Am.*, 11 : 67–89.

CHAPMAN, R. S. (1969). *The insects: structure and functions*. English University Press, London, 819 pp.

CHAPMAN, T. A. (1894). Some notes on the micro-Lepidoptera whose larvae are external feeders, and chiefly on the early stages of *Eriocephala calthella* (Zygaenidae, Limacodidae, Eriocephalidae). *Trans. (R.) ent. Soc. Lond.*, 1894 : 335–350.

CHINA, W.E. (1953). Two new species of the genus *Cyrtopeltis* (Hemiptera) associated with sundews in Western Australia. *W. Aust. Nat.*, 4 : 1–8.

CHRISTIANSEN, K. (1964). Bionomics of Collembola. *A. Rev. Ent.*, 9 : 147–178.

CHRISTOPHERS, S.R. (1960). Aedes aegypti (*L.*) *the yellow fever mosquito*. Cambridge University Press, Cambridge, 739 pp.

CHURCHILL, G.B., JOHN, H.H., DUNEON, D.P. & HODSON, A.C. (1964). Long-term effects of defoliation of aspen by the forest tent caterpillar. *Ecology*, **45** : 630–633.

CLAUSEN, C.P. (1940). *Entomophagous insects*. McGraw-Hill, New York, 688 pp.

CLAYTON, R.B. (1970). The chemistry of non-hormonal interactions: terpenoid compounds in ecology. In Sondheimer, E. & Simeone, J.B. (eds) *Chemical ecology*: 235–280. Academic Press, New York & London.

COAKER, T.H. & FINCH, S. (1972). The association of the cabbage rootfly with its food and host plants (*this volume*).

COBBEN, R.H. (1968). *Evolutionary trends in Heteroptera. Part* 1. *Eggs, architecture of the shell, gross embryology and eclosion*. Pudoc, Wageningen, 475 pp.

COLLYER, E. (1951). The separation of *Conwentzia pineticola* End. from *Conwentzia psociformis* (Curt.), and notes on their biology. *Bull. ent. Res.*, **42** : 555–564.

CROSS, D.J. (1966). *Approaches towards an assessment of the role of insect food in the ecology of game birds especially the partridge* (Perdix perdix). Ph.D. thesis, University of London.

CURRIE, G.A. (1932). Some notes on the biology and morphology of the immature stages of *Harpobittacus tillyardi* (Order Mecoptera). *Proc. Linn. Soc. N.S.W.*, **57** : 116–122.

CURRIE, G.A. (1937). Galls of Eucalyptus trees. A new type of association between flies and nematodes. *Proc. Linn. Soc. N.S.W.*, **62** : 147–174.

DADD, R.H. (1960). The nutritional requirements of locusts—II. Utilisation of sterols. *J. Insect Physiol.*, **5** : 161–168.

DADD, R.H. (1963). Feeding behaviour and nutrition in grasshoppers and locusts. *Adv. Insect Physiol.*, **1** : 47–109.

DADD, R.H. & MITTLER, T.E. (1966). Permanent culture of an aphid on a totally synthetic diet. *Experientia*, **22** : 832.

DADD, R.H. & KRIEGER, D.L. (1967). Continuous rearing of aphids of the *Aphis fabae* complex on sterile synthetic diet. *J. econ. Ent.*, **60** : 1512–1514.

DAVIDSON, J. (1934). The 'Lucerne Flea' *Smynthurus viridis* L. (Collembola) in Australia. *Bull. Commonw. scient. ind. Res. Org.*, no. 79, 66 pp.

DAVIES, W.M. (1928*a*). The bionomics of *Apion ulicis* Forst. (Gorse Weevil) with special reference to its rôle in the control of *Ulex europaeus* in New Zealand. *Ann. appl. Biol.*, **15** : 263–286.

DAVIES, W.M. (1928*b*). The effect of variation in relative humidity on certain species of Collembola. *Br. J. exp. Biol.*, **6** : 79–86.

DAVIES, W.M. (1928*c*). On the economic status and bionomics of *Sminthurus viridis* Lubb. (Collembola). *Bull. ent. Res.*, **18** : 291–296.

DETHIER, V.G. (1954). Evolution of feeding preferences in phytophagous insects. *Evolution, Lancaster, Pa.*, **8** : 33–54.

DETHIER, V.G. (1966). Feeding behaviour. In Haskell, P.T. (ed.) *Insect behaviour*. Symp. R. ent. Soc. Lond., no. 3 : 46–58.

DETHIER, V.G. (1970). Chemical interactions between plants and insects. In Sondheimer, E. & Simeone, J.B. (eds) *Chemical ecology* : 83–102. Academic Press, New York & London.

DETHIER, V.G. & SCHOONHOVEN, L.M. (1969). Olfactory coding by lepidopterous larvae. *Entomologia exp. appl.*, **12** : 535–543.

DIELEMAN, F.L. (1969). Effects of gall midge infestation on plant growth and growth regulating substances. *Entomologia exp. appl.*, **12** : 745–749.

DIXON, A.F.G. (1970). Stabilization of aphid populations by an aphid induced plant factor. *Nature, Lond.*, **227** : 1368–1369.

DRAKE, C.J. (1957). Four new species of gall-making lacebugs (Hemiptera : Tingidae). *Philipp. J. Sci.*, **85** : 471–475.

EASTOP, V.F. (1972). Deductions from the present day host plants of aphids and related insects (*this volume*).

EHRHARDT, P. (1968). Nachweis einer durch symbiontische Mikroorganismen bewirkten Sterinsynthese in künstlich ernährten Aphiden (Homoptera, Rhynchota, Insecta). *Experientia*, **24** : 82–83.

EHRLICH, P.R. & RAVEN, P.H. (1965). Butterflies and plants: a study in co-evolution. *Evolution, Lancaster, Pa*, **18** : 586–608.

EISNER, T. (1970). Chemical defence against predation in arthropods. In Sondheimer, E. & Simeone, J. B. (eds) *Chemical ecology* : 157–217. Academic Press, New York & London.

VAN EMDEN, H. F. & BASHFORD, M.A. (1971). The performance of *Brevicoryne brassicae* and *Myzus persicae* in relation to plant age and leaf amino acids. *Entomologia exp. appl.*, **14** : 349–360.

VAN EMDEN, H.F., EASTOP, V.F., HUGHES, R.D. & WAY, M.J. (1969). The ecology of *Myzus persicae*. *A. Rev. Ent.*, **14** : 197–270.

VAN EMDEN, H.F. & WAY, M.J. (1972). Host plants in the population dynamics of insects (*this volume*).

EVANS, G.O., SHEALS, J.G. & MACFARLANE, D. (1961). *The terrestrial Acari of the British Isles*, **1**. Brit. Mus. Nat. Hist., London, 219 pp.

EVANS, J.W. (1940). Tube-building Cercopids (Homoptera, Machaerotidae). *Trans. R. Soc. S. Aust.*, **64** : 70–75.

EVANS, J.W. (1966). The leafhoppers and froghoppers of Australia and New Zealand. *Mem. Aust. Mus.*, **12** : 1–347.

FEENY, P.P. (1968). Effect of oak leaf tannins on larval growth of the winter moth *Operophtera brumata*. *J. Insect Physiol.*, **14** : 805–817.

FEENY, P.P. (1969). Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. *Phytochemistry*, **8** : 2119–2126.

FEENY, P.P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51** : 565–581.

FEENY, P.P. & BOSTOCK, H. (1968). Seasonal changes in the tannin content of oak leaves. *Phytochemistry*, **7** : 871–880.

FENNAH, R.G. (1963). Nutritional factors associated with seasonal population increase of cacao thrips *Selenothrips rubrocinctus* (Giard) (Thysanoptera), on cashew, *Anacardium occidentale*. *Bull. ent. Res.*, **53** : 681–713.

FINK, D.E. (1914). Injury to truck crops by spring-tails (*Smynthurus* sp.). *J. econ. Ent.*, **7** : 400–401.

FOLSOM, J.W. (1933). The economic importance of Collembola. *J. econ. Ent.*, **26** : 934–939.

FRAENKEL, G. (1953). The nutritional value of green plants for insects. *Trans. 9th Int. Congr. Ent., Amsterdam, 1951*, **2** : 90–100.

FRAENKEL, G. (1959). The raison d'être of secondary plant substances. *Science, N.Y.*, **129** : 1466–1470.

FRAENKEL, G. (1969). Evaluation of our thoughts on secondary plant substances. *Entomologia exp. appl.*, **12** : 473–486.

FRIEND, W.G., SALKELD, E.H. & STEVENSON, I.L. (1959). Acceleration of development of larvae of the onion maggot *Hylemya antiqua* (Meig.) by micro-organisms. *Can. J. Zool.*, **37** : 721–727.

GILL, J.S. & LEWIS, C.T. (1971). Systemic action of an insect feeding deterrent. *Nature, Lond.*, **232** : 402–403.

GILLETT, J.D. & WIGGLESWORTH, V.B. (1932). The climbing organ of an insect, *Rhodnius prolixus* (Hemiptera, Reduviidae). *Proc. Roy. Soc.* (B), **111** : 364–376.

GOODCHILD, A.J.P. (1966). Evolution of the alimentary canal in the Hemiptera. *Biol. Rev.*, **41** : 97–140.

GORDON, H.T. (1959). Minimal nutritional requirements of the German Roach, *Blatella germanica* L. *Ann. N.Y. Acad. Sci.*, **77** : 290–351.

GORDON, H.T. (1961). Nutritional factors in insect resistance to chemicals. *A. Rev. Ent.*, **6** : 27–54.

GRANDI, G. (1929). Studio morfologico e biologico della *Blastophaga psenes* (L.). *Boll. Lab. Ent. R. Ist. sup. agr. Bologna*, **2** : 1–147.

GRESSITT, J.K., AOKI, J. & SAMUELSON, G.A. (1966). Epizoic symbiosis. *Pacif. Insects*, **8** : 221–297.

GRINFEL, E.K. (1959). The feeding of thrips (Thysanoptera) on pollen of flowers and the origin of asymmetry in their mouth parts [In Russian]. *Ênt. Obozr.*, **38** : 798–804.

GYLLENBERG, G. (1970). Energy flow through a simple food chain of a meadow ecosystem in four years. *Annls Zool. Fenn.*, 7 : 283–289.

HABERLANDT, G. (1914). *Physiological plant anatomy* (translated by M.Drummond). Macmillan, London, 777 pp.

HARLOW, P. M. (1956). A study of ovarial development and its relation to adult nutrition in the blowfly, *Protophormia terrae-novae* (R-D.). *J. exp. Biol.*, **33** : 777–797.

HARRIS, P. (1960). Production of pine resin and its effect on survival of *Rhyacionia buoliana* (Schiff.) (Lepidoptera : Olethreutidae). *Can. J. Zool.*, **38** : 121–130.

HARRIS, P. (1972). Insects in the population dynamics of plants (*this volume*).

HASKELL, P.T. & MORDUE, A.J. (1969). The rôle of mouthpart receptors in the feeding behaviour of *Schistocerca gregaria*. *Entomologia exp. appl.*, **12** : 591–610.

HENSON, W.R. & STARK, R.W. (1959). The description of insect numbers. *J. econ. Ent.*, **52** : 847–850.

HERING, E.M. (1951). *Biology of the leaf miners*. W.Junk, The Hague, 420 pp.

HILL, D.S. (1967). *Figs.* (Ficus *spp.*) *of Hong Kong*. Hong Kong University Press, Hong Kong, 130 pp.

HILL, D.S. (1971). Wasps and figs. *New Scient.*, **50** : 144–146.

HILLYER, R.J. (1965). *Some aspects of host relationships of* Oscinella frit *L.* (*Diptera, Chloropidae*). Ph.D. thesis, University of London.

HOCKING, B. (1970). Insect associations with the swollen thorn acacias. *Trans. R. ent. Soc. Lond.*, **122** : 211–255.

HOLLOWAY, J.K. (1964). Projects in biological control of weeds. In DeBach, P. (ed.) *Biological control of insect pests and weeds* : 650–670. Chapman & Hall, London.

HOLWAY, R.T. (1935). Preliminary note on the structure of the pretarsus and its possible phylogenetic significance. *Psyche, Camb.*, **42** : 1–24.

HOUSE, H.L. (1958). Nutritional requirements of insects associated with animal parasitism. *Expl Parasit.*, **7** : 555–609.

HOUSE, H.L. (1961). Insect nutrition. *A. Rev. Ent.*, **6** : 13–26.

HOUSE, H.L. (1965). Effect of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and nutrition of a phytophagous larva, (*Celerio euphorbiae* (Linnaeus)) Lepidoptera : Sphingidae. *Can. Ent.*, **97** : 62–68.

HOUSE, H.L. (1969). Effects of different proportions of nutrients on insects. *Entomologia exp. appl.*, **12** : 651–669.

HSIAO, T.H. (1969). Chemical basis of host selection and plant resistance in oligophagous insects. *Entomologia exp. appl.*, **12** : 777–788.

HUGHES, T.E. (1959). *Mites or the Acari.* Athlone Press, London, 225 pp.

HUKUSIMA, S. (1958). The effect of varying nitrogen levels in nutrition upon the arthropod fauna in young apple trees, with special reference to the increase of the mite and aphid populations. *Bull. Fac. Agric. Hirosaki Univ.*, **4** : 72–79.

IMAI, S., TOYOSATO, T., FUJIOKA, S., SAKAI, M. & SATO, Y. (1968). Screening of plants for compounds with insect moulting activity. *Chem. pharm. Bull., Tokyo*, **17** : 335–339.

IMMS, A.D. (1957). *A general textbook of entomology* (9th ed. revised). Methuen, London, 886 pp.

ISHIKAWA, S., HIRAO, T. & ARAI, N. (1969). Chemosensory basis of hostplant selection in the silkworm. *Entomologia exp. appl.*, **12** : 544–554.

JANZEN, D.H. (1966). Co-evolution of mutualism between ants and acacias in Central America. *Evolution, Lancaster, Pa*, **20** : 249–275.

JANZEN, D.H. (1967*a*). Interaction of the Bulls'-horn Acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F.Smith) in eastern Mexico. *Kans. Univ. Sci. Bull.*, **47** : 315–558.

JANZEN, D.H. (1967*b*). Fire, vegetation structure, and the ant × acacia interaction in Central America. *Ecology*, **48** : 26–35.

JANZEN, D.H. (1969). Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution, Lancaster, Pa*, **23** : 1–27.

JANZEN, D.H. (1971). Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in deciduous tropical forest. *Am. Nat.*, **105** : 97–112.

JENSEN, D.D. (1959). A plant virus lethal to its insect vector. *Virology*, **8** : 164–175.

JERMY, T. (1966). Feeding inhibitors and food preference in chewing phytophagous insects. *Entomologia exp. appl.*, **9** : 1–12.

JOHNSON, B. (1953). The injurious effects of the hooked epidermal hairs of French beans (*Phaseolus vulgaris* L.) on *Aphis craccivora* Koch. *Bull. ent. Res.*, **44** : 779–788.

JOHNSON, B. (1956). The influence on aphids of the glandular hairs on tomato plants. *Pl. Path.*, **5** : 131–132.

JOHNSON, C.G. (1934). On the eggs of *Notostira erratica* L. (Hemiptera, Capsidae). 1. Observations on the structure of the egg and the sub-opercular yolk-plug, swelling of the egg and hatching. *Trans. Soc. Br. Ent.*, **1** : 1–32.

JOHNSON, C.G. (1937). The absorption of water and the associated volume changes occurring in the eggs of *Notostira erratica* L. (Hemiptera, Capsidae) during embryonic development under experimental conditions. *J. exp. Biol.*, **14** : 413–421.

JOHNSON, C.G. (1962). Diseases and pests of cocoa. B.Capsids: a review of present knowledge. In Wills, J.B. (ed.) *Agriculture and land use in Ghana* : 316–331. Oxford University Press, London.

JUNIPER, B.E. & BURRAS, V.K. (1962). How pitcher plants trap insects. *New Scient.*, **13** : 75–77.

KAYUMBO, H. (1963). *The water relations of eggs of some Hemiptera–Heteroptera*. Ph.D. thesis, University of London.

KENNEDY, J.S. (1951). A biological approach to plant viruses. *Nature, Lond.*, **168** : 890.

KENNEDY, J.S. (1953). Host plant selection in Aphididae. *Trans. 9th Int. Congr. Ent., Amsterdam, 1951*, **2** : 106–113.

KENNEDY, J.S. (1958). Physiological condition of the host plant and susceptibility to aphid attack. *Entomologia exp. appl.*, **1** : 50–65.

KENNEDY, J.S. & BOOTH, C.O. (1951). Host alternation in *Aphis fabae* Scop. 1. Feeding preferences and fecundity in relation to the age and kind of leaves. *Ann. appl. Biol.*, **38** : 25–64.

KENNEDY, J.S. & FOSBROOKE, I.H.M. (1972). The plant in the life of an aphid (*this volume*).

KENNEDY, J.S. & MOORHOUSE, J.E. (1969). Laboratory observations on locust responses to wind-borne grass odour. *Entomologia exp. appl.*, **12** : 487–503.

KEVAN, P.G. & KEVAN, D.K.McE. (1970). Collembola as pollen feeders and flower visitors with observations from the high Arctic. *Questiones entomologicae*, **6** : 311–326.

KINSEY, A.C. (1920). Phylogeny of cynipid genera and biological characteristics. *Bull. Am. Mus. nat. Hist.*, **42** : 357–402.

KNIGHT, C.B. & ANGEL, R.A. (1967). A preliminary study of the dietary requirements of *Tomocerus* (Collembola). *Am. Midl. Nat.*, **77** : 510–517.

KULLENBERG, B. (1946). Studien über die Biologie der Capsiden. *Zool. Bidr. Upps.*, **23** : 1–522.

LABEYRIE, V. (1962). Mise en évidence d'influences multiples de la plante hôte sur la stimulation de la ponte chez *Acanthoscelides obtectus* Say. *C.r. Séanc. Soc. Biol.*, **156** : 1473–1477.

LABEYRIE, V. (1970). Signification adaptative de l'integration des signaux fournis par le milieu extérieur lors de l'ovogenèse des insectes. *Colloques int. Cent. natn. Rech. scient.*, **189** : 21–41.

LAWTON, J.H. (1970). Feeding and food energy assimilation in larvae of the damsel fly *Pyrrhosoma nymphula* (Sulz.) (Odonata : Zygoptera). *J. Anim. Ecol.*, **39** : 669–689.

LEIUS, K. (1960). Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Can. Ent.*, **92** : 369–376.

LEPPIK E.E. (1955). *Dichromena ciliata*, a noteworthy entomophilous plant among Cyperaceae. *Am. J. Bot.*, **42** : 455–458.

LEPPIK, E.E. (1957). Evolutionary relationship between entomophilous plants and anthophilous insects. *Evolution, Lancaster, Pa*, **11** : 466–481.

LESTON, D. (1953). 'Phloeidae' Dallas: systematics and morphology with remarks on the phylogeny of 'Pentomoidea' Leach and upon the position of '*Serbana*' Distant (Hemiptera). *Revta bras. Biol.*, **13** : 121–140.

LESTON, D. (1970). Entomology of the cocoa farm. *A. Rev. Ent.*, **15** : 273–294.

LEVIN, D.A. (1971). Plant phenolics: an ecological perspective. *Am. Nat.*, **105** : 157–181.

LEVINSON, Z.H. (1962). The function of dietary sterols in phytophagous insects. *J. Insect Physiol.*, **8** : 191–198.

LIPKE, H. & FRAENKEL, G. (1956). Insect nutrition. *A. Rev. Ent.*, **1** : 17–44.

LLOYD, F.E. (1942). *The carnivorous plants*. Chronica Botanica Co., Waltham, Mass., 352 pp.

LORD, C. (ed.) (1968). *Biochemists' handbook*. Spon, London, 1192 pp.

MA, WEI-CHUN (1969). Some properties of gustation in the larva of *Pieris brassicae*. *Entomologia exp. appl.*, **12** : 584–590.

MACLAGAN, D.S. (1932). An ecological study of the 'lucerne flea' (*Smynthurus viridis* Linn.). *Bull. ent. Res.*, **23** : 101–145.

MALYSHEV, S.I. (1966). *Genesis of the Hymenoptera and the phases of their evolution.* Methuen, London, 319 pp.

MARAMOROSCH, K. (1963). Arthropod transmission of plant viruses. *A. Rev. Ent.*, **8** : 369–414.

MARKS, R.J. (1970). *A study of interactions in an invertebrate predator-prey system.* M.Sc. thesis, University of London.

MARTIN, J.T. & JUNIPER, B.E. (1970). *The cuticles of plants.* E.Arnold, London, 347 pp.

MATOLCSY, G., SARINGER, G.Y., GABORJANYI, R. & JERMY, T. (1968). Antifeeding effect of some substituted phenoxy compounds on chewing and sucking phytophagous insects. *Acta Phytopathol. Acad. Sci. Hung.*, **3** : 275–277.

MCMURTRY, J.A. & SCRIVEN, G.T. (1968). Studies on predator-prey interactions between *Amblyseius hibisci* and *Oligonychus punicae*: Effects of host-plant conditioning and limited quantities of an alternate food. *Ann. ent. Soc. Am.*, **61** : 393–397.

MCNEILL, S. (1971). The energetics of a population of *Leptopterna dolabrata* (Heteroptera : Miridae). *J. Anim. Ecol.*, **40** : 127–140.

MELLANBY, K. & FRENCH, R.A. (1958). The importance of drinking water to larval insects. *Entomologia exp. appl.*, **1** : 116–124.

MERZ, E. (1959). Pflanzen und Raupen. Über einige Prinzipien der Futterwahl bei Grosschmetterlingsraupen. *Biol. Zbl.*, **78** : 152–188.

MILES, P.W. (1968*a*). Studies on the salivary physiology of plant bugs: experimental induction of galls. *J. Insect Physiol.*, **14** : 97–106.

MILES, P.W. (1968*b*). Insect secretions in plants. *A. Rev. Phytopath.*, **6** : 137–164.

MILES, P.W. (1969). Interaction of plant phenols and salivary phenolases in the relationship between plants and Hemiptera. *Entomologia exp. appl.*, **12** : 736–744.

MITTLER, T.E. & SUTHERLAND, O.R.W. (1969). Dietary influences on aphid polymorphism. *Entomologia exp. appl.*, **12** : 703–713.

MONOD, T. & CARAYON, J. (1958). Observations sur les *Copium* (Hemipt. Tingidae) et leur action cecidogêne sur les fleurs de *Teucrium* (Labiées). *Archs Zool. exp. gén.*, **95** : 1–31.

MORDUE, A.J. & HILL, L. (1970). The utilisation of food by the adult female desert locust, *Schistocerca gregaria*. *Entomologia exp. appl.*, **13** : 352–358.

MOROWITZ, H.J. (1968). *Energy flow in biology.* Academic Press, New York & London, 179 pp.

MOUND, L.A. (1963). Host-correlated variation in *Bemisia tabaci* (Gennadius) (Homoptera : Aleyrodidae). *Proc. R. Ent. Soc. Lond.* (A), **38** : 171–180.

MOUND, L.A. (1971). Gall-forming thrips and allied species (Thysanoptera : Phlaeothripinae) from *Acacia* trees in Australia. *Bull. Br. Mus. nat. Hist.* (*Ent.*), **25** : 389–466.

MUKERJI, M.K. & LE ROUX, E.J. (1969*a*). A quantitative study of food consumption and growth of *Podisus maculiventris* (Hemiptera : Pentatomidae). *Can. Ent.*, **101** : 387–403.

MUKERJI, M.K. & LE ROUX, E.J. (1969*b*). A study on energetics of *Podisus maculiventris* (Hemiptera : Pentatomidae). *Can. Ent.*, **101** : 449–460.

NORMAN, A.L. (1936). The composition of forage crops 1. Rye grass. *Biochem. J.*, **30** : 1354–1362.

NUORTEVA, P. (1954). Studies on the salivary enzymes of some bugs injuring wheat kernels. *Suom. hyönt. Aikak.*, **20** : 102–124.

NUORTEVA, P. (1955). On the nature of the plant injuring salivary toxins of insects. *Suom. hyönt. Aikak.*, **21** : 33–38.

NUORTEVA, P. (1956). Studies on the effect of the salivary secretions of some Heteroptera and Homoptera on plant growth. *Suom. hyönt. Aikak.*, **22** : 108–117.

NUORTEVA, P. (1958). Die Rolle der Speichelsekrete im Wechselverhältnis zwischen Tier und Nahrungspflanze bei Homopteren und Heteropteren. *Entomologia exp. appl.*, **1** : 41–49.

NUORTEVA, P. (1962). Studies on the causes of the phytopathogenicity of *Calligypona pellucida* (F.) (Hom., Araeopidae). *Suomal. eläin-ja kasvit. Seur. van. eläin. Julk.*, **23** : 3–58.

OSBORNE, D.J. (1972). Mutual regulation of growth and development in plants and insects (*this volume*).

PACLT, J. (1956). *Biologie der primär flügellosen Insekten.* Gustav Fischer Verlag, Jena, 258 pp.

PAINTER, R.H. (1951). *Insect resistance in crop plants.* Macmillan, New York, 520 pp.

PATHAK, M.D. (1969). Stem borer and leaf hopper-plant hopper resistance in rice varieties. *Entomologia exp. appl.*, **12** : 789–800.

PEARSON, E.O. (1958). *The insect pests of cotton in tropical Africa*. Eastern Press, London, 355 pp.
PENDERGRAST, J.G. (1962). The internal anatomy of the Peloridiidae (Homoptera : Coleorrhyncha). *Trans. R. ent. Soc. Lond.*, **114** : 49–65.
PROSSER, C.L. & BROWN, F.A. (1961). *Comparative animal physiology*. Saunders, Philadelphia & London, 688 pp.
RAMIREZ, W. (1969). Taxonomic and biological studies of neotropical fig wasps (Hymenoptera : Agaonidae). *Kans. Univ. Sci. Bull.*, **49** : 1–44.
RAMIREZ, W, (1970). Host specificity of fig wasps (Agaonidae). *Evolution. Lancaster, Pa*, **24** : 680–691.
RAMSAY, J.A., BUTLER, C.G. & SANG, J.H. (1938). The humidity gradient at the surface of a transpiring leaf. *J. exp. Biol.*, **15** : 255–265.
READSHAW, J.L. (1965). A theory of phasmatid outbreak release. *Aust. J. Zool.*, **13** : 475–490.
REES, C.J.C. (1969). Chemoreceptor specificity associated with choice of feeding site by the beetle, *Chrysolina brunsvicensis* on its food plant, *Hypericum hirsutum*. *Entomologia exp. appl.*, **12** : 565–583.
RIPLEY, L.B. & VAN HEERDEN, P.W. (1939). Further studies on gustatory reactions of the Wattle Bagworm (*Acanthopsyche junodi*, Heyl). *Bull. Dep. Agric. For. Un. S. Afr.*, no. 205, 20 pp.
ROTHSCHILD, M. (1972). Secondary plant substances and warning colouration in insects (*this volume*).
RUSSELL, F.C. (1947). The chemical composition and digestibility of fodder shrubs and trees. *Jt. Publs Commonw. agric. Bur.*, **10** : 185–231.
RUSSELL, M.C. (1953). Notes on insects associated with sundews (*Drosera*) at Lesmurdie. *W. Aust. Nat.*, **4** : 9–12.
SANG, J.H. (1959). Circumstances affecting the nutritional requirements of *Drosophila melanogaster*. *Ann. N.Y. Acad. Sci.*, **77** : 352–365.
SCHNEPF, E. (1966). Feinbau und Funktion pflanzlicher Drüsen. *Umschau*, **66** : 522–527.
SCHOONHOVEN, L. M. (1969*a*). Amino acid receptor in larvae of *Pieris brassicae* (Lepidoptera). *Nature, Lond.*, **221** : 1268.
SCHOONHOVEN, L.M. (1969*b*). Gustation and food-plant selection in some lepidopterous larvae. *Entomologia exp. appl.*, **12** : 555–564.
SCHOONHOVEN, L. M. (1972). Plant recognition by lepidopterous larvae (*this volume*).
SERNANDER, R. (1906). Entwurf einer Monographie der europäischen Myrmekochoren. *K. svenska Vetensk-Akad. Handl.*, **41**, no. 7, 410 pp.
SINGH, S.B. (1969). Preliminary observations on the food preference of certain Collembola (Insecta). *Revue Écol. Biol. Sol*, **6** : 461–467.
SLAMA, K. (1969). Plants as a source of material with insect hormone activity. *Entomologia exp. appl.*, **12** : 721–728.
SMART, J. & HUGHES, N.F. (1972). The insect and the plant: progressive palaeoecological integration (*this volume*).
SMITH, D.S. & NORTHCOTT, F.E. (1951). The effects on the grasshopper, *Melanoplus mexicanus mexicanus* (Sauss.) of varying the nitrogen content of its food plant. *Can. J. Zool.*, **29** : 297–304.
SOO HOO, L.F. & FRAENKEL, G. (1966). The selection of food plants in a polyphagous insect, *Prodenia eridania* (Cramer). *J. Insect Physiol.*, **12** : 693–709.
SOUTHWOOD, T.R.E. (1955). *Some studies on the systematics and ecology of Heteroptera*. Ph.D. thesis, University of London.
SOUTHWOOD, T.R.E. (1956). The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. *Trans. R. ent. Soc. Lond.*, **108** : 163–221.
SOUTHWOOD, T.R.E. (1960). The abundance of the Hawaiian trees and the number of their associated insect species. *Proc. Hawaii. ent. Soc.*, **17** : 299–303.
SOUTHWOOD, T.R.E. (1961*a*). The number of species of insect associated with various trees. *J. Anim. Ecol.*, **30** : 1–8.
SOUTHWOOD, T.R.E. (1961*b*). The evolution of the insect-host tree relationship—a new approach. *Proc. 11th Int. Congr. Ent., Vienna, 1960*, **1** : 651–654.
SOUTHWOOD, T.R.E. & BLACKITH, R.E. (1960). Inter- and intra-specific variation in the mirid genus *Plagiognathus*. *Proc. R. ent. Soc. Lond.* (C), **25** : 9–10.
SOUTHWOOD, T.R.E. & LESTON, D. (1959). *Land and water bugs of the British Isles*. Warne, London, 436 pp.
SPECTOR, W.S. (ed.) (1956). *Handbook of biological data*. Saunders, Philadelphia & London, 584 pp.
SPENCER, K.A. (1971). Introduction to the biology, evolution and world distribution of the Agromyzidae (Diptera). *Proc. R. ent. Soc. Lond.* (C), **35** : 33–34.

STAHL, E. (1888). Pflanzen und Schnecken. Biologische Studie über die Schutzmittel der Pflanzen gegen Schneckenfrass. *Jena Z. Med. Naturw.*, **22** : 557–684.

STARK, R.W. (1965). Recent trends in forest entomology. *A. Rev. Ent.*, **10** : 303–324.

STEINHAUS, E.A. (1946). *Insect microbiology*. Comstock Pub. Co., New York, 763 pp.

STEINHAUS, E.A. (1963). *Insect pathology* (2 volumes). Academic Press, New York & London, 661 & 689 pp.

STRICKLAND, A.H. (1960). Ecological problems in crop pest control. In Wood, R.K.S. (ed.) *Biological problems arising from the control of pests and diseases*. Symp. Inst. Biol., no. 9 : 1–13.

TANTON, M.T. (1962). The effect of leaf 'toughness' on the feeding of larvae of the mustard beetle. *Entomologia exp. appl.*, **5** : 74–78.

TAYLOR, L.R. (1959). Abortive feeding behaviour in a black aphid of the *Aphis fabae* group. *Entomologia exp. appl.*, **2** : 143–153.

THOMPSON, W.R. (1954). Biological control work on cedar scales in Bermuda. *Rep. 6th Commonw. ent. Conf., 1954* : 89–95.

THORSTEINSON, A.J. (1960). Host selection in phytophagous insects. *A. Rev. Ent.*, **5** : 193–218.

THURSTON, R., SMITH, W.T. & COOPER, B.P. (1966). Alkaloid secretion by trichomes of *Nicotiana* species and resistance to aphids. *Entomologia exp. appl.*, **9** : 428–432.

TINSLEY, T.W. (1972). Origins of vector-borne plant viruses (*this volume*).

VANDERZANT, E.S. (1958). The amino acid requirements of the pink bollworm. *J. econ. Ent.*, **51** : 309–311.

VANDERZANT, E.S. & REISER, R. (1956). Studies of the nutrition of the pink bollworm using purified caesin media. *J. econ. Ent.*, **49** : 454–458.

WALDBAUER, G.P. (1968). The consumption and utilization of food by insects. *Adv. Insect Physiol.*, **5** : 229–288.

WALTERS, M.C. (1968). A study of *Sminthurus viridis* (L.) (Collembola) in the Western Cape Province. *Entomology Mem. Dep. Agric. Un. S. Afr.*, no. 16, 99 pp.

WAY, M.J. (1953*a*). Studies on *Theraptus* sp. (Coreidae), the cause of gumming disease of coconuts in East Africa. *Bull. ent. Res.*, **44** : 657–667.

WAY, M. J. (1953*b*). The relationship between certain ant species with particular reference to biological control of the coreid *Theraptus* sp. *Bull. ent. Res.*, **44** : 669–691.

WAY, M.J. (1968). Intra-specific mechanisms with special reference to aphid populations. In Southwood, T.R.E. (ed.) *Insect abundance*. Symp. R. ent. Soc. Lond., no. 4 : 18–36.

WEARING, C.H. (1967). Studies on the relations of insect and host plant II. Effects of water stress in host plants on the fecundity of *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). *Nature, Lond.*, **213** : 1052–1053.

WEARING, C.H. & VAN EMDEN, H.F. (1967). Studies on the relations of insect and host plant I. Effects of water stress in host plants on infestation by *Aphis fabae* Scop., *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). *Nature, Lond.*, **213** : 1051–1052.

WEATHERLEY, P.F., PEEL, A.J. & HILL, G.P. (1959). The physiology of the sieve tube. *J. exp. Bot.*, **10** : 1–16.

WENT, F.W. (1970). Plants and the chemical environment. In Sondheimer, E. & Simeone, J.B. (eds) *Chemical ecology* : 72–81. Academic Press, New York & London.

WHITE, T.C.R. (1969). An index to measure weather-induced stress of trees associated with outbreaks of Psyllids in Australia. *Ecology*, **50** : 905–909.

WHITEHEAD, F.E. & MINER, F.D. (1944). The biology and control of the camel cricket, *Daihinia brevipes*. *J. econ. Ent.*, **37** : 573–581.

WIEGERT, R.G. (1964). Population energetics of meadow spittle-bugs (*Philaenus spumarius* L.) as affected by migration and habitat. *Ecol. Monogr.*, **34** : 217–241.

WIEGERT, R.G. (1965). Energy dynamics of the grasshopper populations in old field and alfalfa field ecosystems. *Oikos*, **16** : 161–176.

WIEGERT, R.G. & EVANS, A.C. (1967). Investigations of secondary productivity in grasslands. In Petrusewicz, K. (ed.) *Secondary productivity of terrestrial ecosystems*, **2** : 499–518. Państwowe Wydawnictwo Naukowe, Warszawa & Crackow.

WIGGLESWORTH, V.G. (1963). *The principles of insect physiology* (4th ed.). Methuen, London, 741 pp.

WILLIAMS, C.M. (1970). Hormonal interactions between plants and insects. In Sondheimer, E. & Simeone, J.B. (eds) *Chemical ecology* : 103–132. Academic Press, New York & London.

WOMERSLEY, H. (1939). *Primitive insects of South Australia*. S. Australian Branch of the British Science Guild, Adelaide, 322 pp.

Wood, D.L. (1962). The attraction created by males of a bark beetle, *Ips confusus* (Le Conte) attacking ponderosa pine. *Pan-Pacif. Ent.*, **38** : 141–145.

Wood, D.L. (1972). Selection and colonization of ponderosa pine by bark beetles (*this volume*).

Yamamoto, R.T., Jenkins, R.Y. & McClusky, R.K. (1969). Factors determining the selection of plants for oviposition by the tobacco hornworm, *Manduca sexta*. *Entomologia exp. appl.*, **12** : 504–508.

Yeo, P.F. (1972). Floral allurements for pollinating insects (*this volume*).